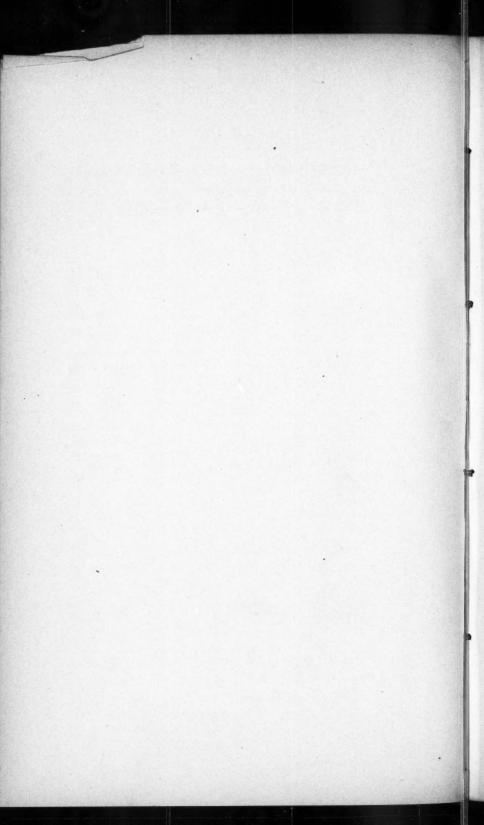
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FEEDING REACTIONS OF THE ROSE CORAL (ISOPHYLLIA).

By F. W. CARPENTER.



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INTRODUCTION.

A NUMBER of investigators have studied in detail the structure of the polyps of the Madreporaria, the group of corals which includes the great majority of reef-building forms. Comparatively little attention has been paid, however, to the activities of the living zooids, although the ultimate result of these activities, the formation of immense quantities of limestone, is a remarkable biological phenomenon, and one of very considerable geological importance.

The present paper is intended as a contribution to the field of coral physiology, and is concerned mainly with the reactions which follow the stimulation of the polyp by means of nutrient substances. Since the corals belong to the phylum of the Coelenterata, in which we have learned to look for the first appearance of a differentiated mechanism for neuro-muscular reflexes, the facts here recorded have at least an incidental bearing on the question of the phylogenetic origin of the nervous system.

The work on which the paper is based was done at the Bermuda Biological Station for Research in the summer of 1909. During a period of several weeks, observations were made on the feeding behavior of rose-coral polyps belonging to the genus Isophyllia. Of this genus three species are recorded by Verrill (: 02) for the Bermuda Islands, viz., dipsacea, fragilis, and multiflora, the first two being much more common than the last. Since the specific characters lie in the skeleton, it is not possible to determine with certainty the species of a living colony, but it is known from the subsequent examination of several skeletons that dipsacea occurred in the material used, and in all probability fragilis was also represented. The question of species

¹ Contributions from the Bermuda Biological Station for Research, No. 20; also Contributions from the Zoölogical Laboratory, University of Illinois, under the direction of Henry B. Ward, No. 4.

is here an unimportant one, as the feeding reactions of the various members of the genus are doubtless essentially the same.

The rose corals at Bermuda form small convex colonies, seldom measuring more than five or six inches in diameter. They occur abundantly in shallow water near shore, often in quiet bays partially shut off from the open sea, where the plankton, which apparently furnishes them with food, is considerably diminished in quantity. Their suc-

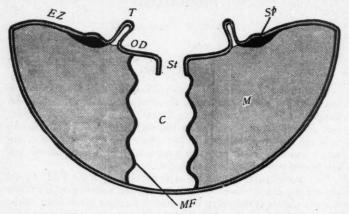


FIGURE 1. Diagrammatic vertical section through an expanded polyp. C, coelenteron or gastrocoelomic cavity; EZ, edge zone; M, mesentery; MF, mesenterial filament; OD, oral disk; Sp, sphincter muscle; St, stomodaeum; T, tentacle.

cessful adaptation to these apparently unfavorable situations, in which most corals do not thrive, suggests a very efficient mechanism for availing themselves of such food as may be present.

The individual polyps of the rose-coral colony are comparatively large, the oral surface often measuring an inch in diameter. The structural features of this surface are shown in the Plate, which is from a photograph of a small portion of a partially expanded colony. In the center of the polyp is the mouth (M), a small oval or circular aperture, which opens into the stomodaeum. Bordering the mouth is the flat ciliated oral disk (OD). This is bounded by a circle of short tentacles (T), external to which is a thickened ciliated edge zone (EZ), raised somewhat above the level of the oral disk, and forming the wide rim which completes the oral surface peripherally. A diagrammatic vertical section through an expanded polyp (Figure 1) reveals its cup-

like shape, and shows the short stomodaeum (St) leading into the coelenteron (C), which is partially subdivided by the radially placed mesenteries (M). Each mesentery, whether complete or incomplete, bears along its free edge a coiled mesenterial filament (MF). The inner margin of the edge zone in such a section shows the cut ends of a large circular endodermal muscle (Sp), which acts as a sphincter. In his monograph on West Indian madreporarian polyps, Duerden (:02) states that this sphincter muscle is more strongly developed in Isophyllia than in any other genus of corals studied by him.

Owing to its large size the rose-coral polyp lends itself readily to a study of its reactions to food materials. The colonies thrive well in the laboratory, where they may be kept alive in running sea-water for weeks. The best time for experimenting is at night, when the polyps become fully expanded, and remain so in diffuse artificial light. However, during the daytime all the feeding reactions may be obtained from the partially contracted polyps, except those of the tentacles, the latter then being withdrawn under the cover of the inner margin of

the edge zone.

THE FEEDING REACTIONS.

Movements of Oral Surface and Mesenteries. When a stream of seawater gently ejected from a pipette falls on the oral disk of a polyp, there is usually no perceptible response. If a drop of a concentrated solution of Liebig's extract of meat in sea-water is similarly applied, there is an immediate contraction of the retractor muscles of the mesenteries, which draws the oral disk downward. Simultaneously a vigorous contraction of the sphincter muscle takes place, and the edge zone is drawn inward over the oral region, above which it forms a temporary roof (Figure 2). Under the influence of a strong stimulus the constantly diminishing central opening in this roof may finally be obliterated by the meeting of the edges of the aperture, and the oral disk below may thus become completely hidden from sight.

Eversion of Stomodaeum and Extrusion of Mesenterial Filaments. While this muscular reaction is taking place, and before the oral disk is concealed, the stomodaeum may be observed to become everted, and to project into the supra-discal space (Figure 2). The eversion of the stomodaeum is accompanied by the extrusion of mesenterial filaments through the mouth, together with the portions of the mesenteries to which they are attached. Not only are mesenterial filaments thrust through the oral aperture, but they are also extruded through the discal wall itself (Figure 2). Duerden (:02), who has observed this behavior of the mesenterial filaments in many madreporarian polyps,

is convinced by his histological studies that there are, however, no permanent port-holes, or cinclides, in the body wall. He believes the mesenterial filaments may make temporary apertures for themselves in any part of the oral disk or wall of the column. When the filaments are withdrawn the orifices close after a few minutes, and leave no traces of their former existence.

The eversion of the stomodaeum, accompanied by partial extrusion of mesenterial filaments through the mouth, may follow a much less

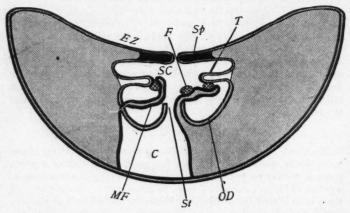


FIGURE 2. Diagrammatic vertical section through a contracted feeding polyp.

C, coelenteron; EZ, edge zone, folded over; F, food particle; MF, mesenterial filament, extruded; OD, oral disk; Sp, sphincter muscle, contracted; St, stomodaeum, everted; SC, supra-discal cavity; T, tentacle.

vigorous stimulus than the one just described. The reaction occurs when a piece of filter paper soaked in diluted meat juice is dropped on the oral disk. The latter becomes depressed, although the stimulus is not sufficient to cause an overfolding of the edge zone. Under these conditions the gullet may be seen to stretch toward the stimulating object. If it reaches the filter paper, this may become partially inclosed by the everted stomodaeum, and may lie for some time in contact with the mesenterial filaments emerging from it, without being actually swallowed. On comparatively few occasions have the bits of filter paper been observed to pass into the coelenteron of the polyp.

Reactions of the Tentacles. After sundown the tentacles of rose-coral

polyps kept in the laboratory become expanded, and may be experimented upon in diffuse artificial light. If exposed to the direct rays of an acetylene bicycle lamp the tentacles contract after a few minutes, but they remain extended in diffuse light of sufficient intensity to render

them clearly visible to the observer.

When the knob-like extremity of a tentacle is touched with a splinter of wood the latter immediately becomes affixed to the end of the tentacle, which is known to be loaded with nematocysts. Possibly the wood is empaled by the numerous nematocyst threads, or it may be held by some adhesive substance. However this may be, the splinter becomes so securely fastened that considerable force is needed to pull it away. A tentacle will often be drawn out two or three times its own length before the splinter is freed, and I have sometimes feared it would be torn from the body in the operation.

If an expanded tentacle is touched on one side with the splinter, there is a quick muscular response to the contact stimulus. The tentacle immediately bends in the direction of the stimulating object, which it

affixes to the terminal knob.

Similar results follow the use of a bit of filter paper in place of the splinter, but if the paper is first dipped in meat extract, in addition to the tentacular reaction the oral disk begins to sink and the edge zone to fold over. In this reflex the distance of the receptor (the end of the tentacle) from the effector (the endodermal body muscles) is worthy of note.

Action of the Cilia. Both the oral disk and the edge zone are abundantly provided with cilia. Carmine particles dropped anywhere on their surfaces are rapidly transferred to the outer margin of the polyp, showing that the usual beat of the cilia is toward the periphery. Carmine particles dropped at the very margin of the mouth pass immediately into the stomodæum, the cilia of which appear to beat constantly inward.

When carmine grains which have previously been soaked in meat extract are dropped on the oral disk they also are usually carried to the peripheral margin of the polyp, even though the stimulation of the nutrient material may be sufficient to cause a slow sinking of the oral surface. I repeated this experiment many times with different polyps, and occasionally succeeded in obtaining a reversal of the cilia, which caused the carmine grains to move toward, and not away from, the I was, however, unable to obtain consistent reactions, and never could predict what the result would be. Analyses of the brand of meat extract used (Liebig's) indicate that it contains several of the substances shown by Parker (: 05a and : 05b) to be the effective stimuli

in producing a reversal of the cilia on the lip zone of Metridium. Of these substances potassium chloride, creatine, and albumoses are present in the extract (Street: 08). The failure to obtain uniform reversals may have been due to the varying differences in the degree of dilution of the stimulating materials, or to unknown factors associated with the physiological condition of the polyps. As will be seen later, ciliary action plays an insignificant part in the feeding process of the rose coral, so that a prompt and definite reversal of the cilia of the oral disk is not a necessary factor in the operation of securing food.

Normal Feeding Behavior. This brief analysis of the responses of the polyp to chemical and tactile stimuli leads to an understanding of the way in which these various reactions are combined in normal feed-

ing behavior.

It is generally believed that coral polyps take as food the small organisms found in the marine plankton, although there is little direct evidence in support of this view. Examination of the coelentera of preserved specimens rarely reveals food material, the scarcity of which in the digestive cavities of the Madreporaria has been commented upon by Duerden, Hickson, Bourne, and Fowler (Pratt: 05). It has even been suggested that the zoöchlorellæ living in symbiotic relation with many corals may elaborate a part of the latter's food, and thus com-

pensate for deficiencies in the supply from outside.

On the other hand it is to be noted that the diurnal expansion and contraction of coral polyps—their alternating periods of activity and quiescence—coincide respectively with the appearance and disappearance of the plankton in the surrounding waters. This can readily be observed in the case of the rose corals. During the daytime, when the sea about them is comparatively free from small organisms, the polyps appear partially contracted. No tentacles are to be seen. But after dark, when the myriad components of the plankton begin to swarm in the water, one may wade along the shore at low tide, and with the aid of a water glass and light from a bicycle lamp, he may readily see that the polyps are fully expanded, with tentacles well out. They have every appearance of being on the alert for food.

In order that I might observe under favorable conditions a polyp in the act of feeding upon what we may suppose to be its natural food, I placed a small colony in a dish of sea-water under a low-power binocular microscope. This was done by lamplight at about half-past nine in the evening when the polyps were well expanded. I then poured into the dish a small quantity of living plankton which a half hour before had been obtained with a tow-net in the locality from which the corals had been collected. The plankton consisted of small Crustacea, including

many copepods, larvæ of various kinds, Protozoa, and other minute marine organisms. Almost immediately the tentacles of the polyp under observation began to turn in various directions. Most of the forms in the plankton were too small to be followed by the eye under the low-power lenses used, but I actually saw one copepod struck by and affixed to the knobbed end of a tentacle. Many organisms doubtless struck against the oral surface of the polyp. In a very few seconds the stomodæum became everted, mesenterial filaments were protruded, the disk sank, and the edge zone commenced to fold in toward the center. The latter movement continued until the tentacles and oral disk were completely roofed over and concealed from sight. In this condition the

polyp remained for some time.

What takes place within the contracted polyp during this period of quiescence cannot be directly observed. But it seems to me highly probable that most of the organisms caught and held by the tentacles, or trapped by the overfolded edge zone, do not reach the gastrocolomic cavity. I believe they are retained in the superficial chamber bounded by the oral disk below and the overfolded edge zone above, and here digested through contact with the extruded mesenterial filaments. The latter are known to be the digestive organs of the Actinozoa. They act upon proteid food by means of a tryptic ferment contained in the secretions of their gland cells, and then ingest or absorb the partially or wholly digested material (Jordan, :07; Pratt, :05). The mesenterial filaments can easily reach to all parts of the superficial chamber, and so be brought into contact with the food held by the tentacles. The attachment of the organisms to the tentacles appears from experiment to be so secure that it is difficult to see how the captured bodies can be discharged except by being digested away.

The mesenterial filaments are themselves well supplied with nematocysts, and these may be useful in securing any free organisms met with in the upper chamber. A few such organisms which are still at liberty to move may make their way into the diminished collenteron, although the cilia of the everted stomodaeum are no longer in a position to produce inhalent currents; but it seems probable that the greater part of the plankton captured by the polyp undergoes extra-coelenteric digestion

in the way described.

When, under natural conditions, the polyp is feeding on small organisms, it is probable that a number of these must be captured by the tentacles, or come into contact with the oral disk, before a cumulative stimulus is obtained sufficient to cause the contraction of the sphincter and mesenterial muscles, and the extrusion of the mesenterial filaments. A few small carmine grains soaked in meat extract and dropped on the

oral disk fail to bring about muscular reactions, even though the granules come into contact with the tentacles when being carried peripherally by the surface cilia. Furthermore, unless the stimulus is a strong one, the edge zone will not fold inward far enough to form a complete roof. As has been seen, a piece of filter paper soaked in dilute meat extract is not a sufficient stimulus to bring about the contraction of the sphincter muscle, although it does cause a sinking of the oral disk, with eversion of the gullet, and partial extrusion of mesenterial filaments through the mouth. But the roofing over of the oral disk is not a necessary part of the process of extra-coelenteric digestion, provided the food organisms are prevented from escaping by the tentacles or by the mesenterial filaments themselves.

As may now be seen, the cilia of the oral surface apparently play an unimportant rôle in the feeding process. Their chief function seems to be that of keeping the oral surface clean. Their abundance, and their persistency in driving foreign particles toward the periphery, may be correlated with the comparatively small amount of surface mucus, which in such polyps as Favia and Fungia forms a well-developed protective

layer over the oral disk (Duerden, : 06).

After the rose-coral polyp has completed the digestion of its food in the supra-discal cavity, the stomodaeum and mesenterial filaments are retracted, and the sphincter and mesenterial muscles relaxed. Water is then drawn in through the mouth by the action of the stomodaeal cilia, and the polyp expands into its resting condition. The cilia of the oral surface now come into play, and transport peripherally any undigested particles that may have been left on the oral disk. Such particles, as may be seen by watching carmine grains, are carried across the edge zone, and deposited in the grooves (IG, Plate) which separate adjacent

polyps.

Feeding Reactions in Other Corals. In its method of taking food, as above described, the rose-coral zoöid differs from the polyps of the three other madreporarian genera whose feeding reactions have been observed. Two of these, Favia and Fungia, were studied by Duerden (:06) in the Hawaiian Islands. The oral disks of Favia and Fungia are not ciliated, but are well provided with gland cells, which secrete on the external surface an abundant coating of mucus. In this mucus foreign particles become embedded. Ordinarily the beat of the stomodaeal cilia is outward, but under the stimulus of meat juice the cilia reverse, and the strong inhalent currents thus produced waft into the mouth shreds and patches of the mucus, together with the foreign materials entangled or embedded in it. The writer evidently considers that these foreign materials furnish the polyp with its food.

The feeding reactions of the third genus, Caryophyllia, have been described briefly by Carlgren (:05). The cilia of the oral surface of this coral beat inward near the mouth, and outward in the peripheral region external to the tentacles. Food is brought by tentacular action into the circum-oral region, whence it is conveyed by cilia to the mouth and stomodaeum. Contractions of the oral disk and peristaltic movements of the gullet assist in the swallowing of large objects.

The feeding process in the related group of aleyonarian corals has been studied by Pratt (:05), who shows that in Aleyonium digitatum food is taken into the gastro-coelomic cavity by means of the muscular activities of the tentacles and gullet. Cilia are not mentioned as being concerned in the process. Within the body of the zooid both intercellular and intracellular digestion take place through the agency of

the mesenterial filaments.

It therefore appears that in all coral polyps heretofore investigated the food reaches the coelenteron and is here digested by the mesenterial filaments. But in Isophyllia the evidence points to an improvement in the method of appropriating food, which makes the polyp of this genus a very efficient plankton trap. It apparently does not risk losing its prey by attempting to transfer it by tentacular or ciliary movements to the mouth, and thence through the gullet to the usual digestive cavity. On the contrary, it affixes its prey firmly to its tentacles, and then, inclosing its captives in a more or less complete, though temporary, chamber formed on the external surface, it proceeds, by means of its mesenterial filaments, to digest its food in situ.

Allusion has been made to the statements of the morphologists in regard to the scarcity of food fragments in the coelenters of preserved madreporarian polyps. Whatever the reason for this may be in the case of other corals, in Isophyllia the failure to find such materials is readily explained by the extra-coelenteric digestion of at least the

greater part of its food.

Evidences of Nervoid Transmission. The term "nervoid" is here used in preference to "nervous" because of the failure of the histologists to demonstrate differentiated tissues of undoubted nervous character in the polypal wall of the great majority of the Madreporaria, including Isophyllia. Duerden (:02) mentions the presence of a distinct ectodermal nerve layer in the tentacles of some species,—"Cladocera, Madrepora, and probably others,"—but in his special description of a representative of the genus Isophyllia no reference is made to such a layer. A weak ectodermal muscle layer seems, however, to be of constant occurrence in the tentacles of the Madreporaria. As far as the polypal wall is concerned, Duerden and Ayres (:05) state

that previous to their discovery of differentiated ectodermal nervous tissue in Coenopsammia no ectodermal columnar nerve or muscle layer had been found in any madreporarian polyp.

In spite of the apparent absence of adjustor tissues in the body wall of Isophyllia, a transmission of at least a nervoid character takes place from receptor to effector through intervening portions of the body. The evidence for this rests on the results of experiments with both chemical and tactile stimuli.

As has been stated in the preceding pages, the application of meat extract to the surface ectoderm is followed by an immediate contraction of the sphincter and mesenterial muscles, both of which are, according to Duerden (:02), situated in the endoderm. An impulse of some kind must, therefore, pass through the intervening mesogloea, which in Isophyllia is a layer of considerable thickness.

A longer distance must be traversed by the nervoid impulse when the retractor muscles of the mesenteries respond to a chemical stimulus affecting the distal end of a tentacle. This reaction, following the application of a bit of filter paper dipped in meat juice, has already been described.

There is evidence, furthermore, that the transmission of impulses is not confined to the polyp stimulated, but may extend throughout the colony. When meat extract is applied to a single polyp a wide-spread effect is produced. For example, in one experiment a small amount of concentrated meat extract was placed during the daytime on the central polyp of a colony with twenty-five oral apertures. The stimulating material soon spread over two adjacent polyps, which, with the central one, became tightly contracted. Meanwhile stomodaea began to be everted and mesenterial filaments extruded all over the colony, which in consequence presented, after two or three minutes, a very ragged appearance. The sphincter and retractor muscles of these outlying polyps were not appreciably affected.

It must be admitted that the explanation of this reaction as due to nervoid impulses from the central polyps is open to the objection that the stimulus may have been local, owing to the diffusion of the meat juice externally over the surface of the colony, or internally through the communicating coelentera. This objection cannot be raised, however, in the case of a colonial reaction induced by a tactile stimulus applied to a single polyp. Especially at night, when the corals are most sensitive, the touching of a centrally situated polyp with a piece of wood or a glass rod will often be followed not only by an immediate local muscular response, but also by a sudden contraction of the mesenterial muscles throughout the colony. The result is seen in the general sinking of the oral surfaces.

While the reaction in the zooid actually touched might be accounted for by the direct stimulation of the endodermal muscles by mechanical pressure exerted through the overlying tissues, this explanation will not apply to the reaction in distant polyps. Nor can the movements in the outer portions of the colony be the result of the strain exerted by the contracting central polyp on contiguous polyps, and by these, when they in turn contract, on zooids still more distant. For, as we have seen, a central polyp in a colony, contracting because of the direct application of a chemical stimulus, does so without affecting the retractor muscles of neighboring polyps. And, finally, the wide-spread reaction cannot be explained by assuming that the protoplasm of the colony is remarkably sensitive to slight molecular vibrations set up in it by touching one of the polyps. If this were so, the colonies would constantly be responding by obvious muscular contractions to vibrations in the surrounding medium or in the solid substratum on which they rest. That such reactions do not occur is evident from repeated observation.

When we turn from these experimental evidences of nervoid transmission to the histology of the Madreporaria, our attention is naturally directed to the mesogloea, through which we infer the impulses must pass, and in which we should, therefore, expect to discover at least some trace of transmitting tissues. According to Duerden (:02) "the mesogloea of coral polyps has generally been described as a perfectly structureless layer"; but the following quotation from page 416 of his monograph on West Indian Madreporaria shows that this statement does not hold for the form with which we are concerned:

"In large polyps, such as *Isophyllia dipsacea*, and also in Maeandrina, the mesogloea is rather thick, and minute connective-tissue cells occur sparsely throughout. In sections the cells are circular or oval in shape, with a central nucleus, and minute prolongations extend in all directions; many of these reach one or other of the surfaces of the layer, and there come into contact with the ectodermal or endodermal cells. In some instances the processes extend right across from one layer to the other, but are mostly disposed in an irregular stellate manner."

These "connective-tissue cells" are probably homologous with those forming the mesoglocal cell plexus in the related Aleyonaria. This plexus was formerly considered to be nervous in function, but the studies of Pratt (:05) on the digestive organs of the Aleyonaria indicate that the amoeboid cells whose processes give rise to the network are concerned with the ingestion and transportation of food. By means of these wandering cells "nutriment may be conveyed from the diges-

tive endoderm cells of the zoöids to every portion of the colony." The system, therefore, in the opinion of the writer, "must be regarded as a nutritive as well as a sensitive plexus." More recently Kassianow (:08) has demonstrated in Alcyonium digitatum a well-developed ectodermal nervous system with ganglion and sense cells. He denies a

nervous function to the branched cells of the mesogloea.

Returning to the histological structure of Isophyllia, it can be said that the so-called "connective-tissue cells" which bridge the mesogloea from ectodermal receptors to endodermal effectors fulfill, topographically at least, the requirements of a primitive correlating segment in a reflex mechanism. The ontogenetic history of these cells, and their exact structural interrelations, have not been worked out, so far as I am aware. But the alluring theory presents itself that these branching cells have migrated from the ectoderm, and, spreading throughout the mesogloea, have assumed contact relations one with another by means of their processes; and though they may not have become highly specialized nervous elements, we may suppose that their protoplasm has retained and augmented its primitive endowment of irritability. Possibly other primitive amoeboid characters have also been retained, such as the capacity for ingesting food, or for moving about by means of pseudopods, - both of which are suggested by Pratt's observations on the cells of the mesogloeal plexus of Alcy-

The theory of the phylogenetic origin of the nervous system as outlined by Parker (: 10), calls for the appearance of an adjustor tissue made up of primitive synaptic neurones as the next step in the process after the development of a sub-ectodermal nervous network, such as occurs in sea-anemones. Future studies, especially those of a histogenetic character, may reveal that this condition is realized in the loose aggregation of branching cells found in the mesogloea of coral polyps.

SUMMARY.

1. When the rose-coral polyp is stimulated by the application of concentrated meat extract to the oral disk, the latter is drawn downward by the contraction of the retractor muscles of the mesenteries, and the margin of the oral surface is folded inward over the disk by the action of a well-developed sphincter muscle.

Meanwhile the stomodaeum is everted, and the mesenterial filaments are extruded both through the mouth and through temporary

apertures in the oral disk.

3. The tentacles react quickly to contact stimulation, and affix the object which touches them to their knob-like distal ends, which are

heavily loaded with nematocysts. When the end of a tentacle is chemically stimulated with meat extract, the retractor muscles of the

polyp contract.

4. Carmine grains dropped on the oral surface of an expanded polyp are transferred by ciliary action to the periphery. When the particles of carmine have previously been soaked in meat juice, the cilia usually continue to beat in an outward direction; occasionally, however, they reverse their effective strokes. The chief function of the cilia seems

to be that of keeping the oral surface clean.

5. When plankton is fed to a polyp the small organisms are affixed by the tentacles, the oral disk sinks, and the marginal zone folds inward until it completely roofs over the tentacles and the depressed oral disk. Into the superficial chamber thus formed, the stomodaeum and mesenterial filaments project, and here the mesenterial filaments, which are the digestive organs of the polyp, probably digest and ingest or absorb the captured plankton, little of which appears to find its way into the reduced gastro-coelomic cavity. Extra-coelenteric digestion apparently takes place, therefore, in rose-coral polyps.

6. There is experimental evidence of the transmission of impulses of at least a nervoid character from ectodermal receptor cells through the mesogloea to endodermal effectors (muscles). This transmission is not confined to a single polyp, but may pass from one polyp to another.

7. It is known that branching cells (so-called "connective-tissue cells") occur in the mesogloea of Isophyllia. These extend from the ectoderm to the endoderm, and so have the topographical relations of adjustor cells, placing the receptor in communication with the effector. In the absence of exact information as to the origin, mutual relationships, and functions of these cells, it is nevertheless suggested that future studies may show them to be primitive synaptic neurones.

BIBLIOGRAPHY.

Carlgren, O.

:05. Ueber die Bedeutung der Flimmerbewegung für den Nahrungstransport bei den Actiniarien und Madreporarien. Biol. Centralbl., Bd. 25, No. 8, pp. 308-322.

Duerden, J. E.

:02. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci., vol. 8, 7th memoir, Washington, pp. 399-600, 25 pls.

Duerden, J. E.

 The Rôle of Mucus in Corals. Quart. Jour. Micr. Sci., vol. 49, n. s., no. 196, pp. 591-614.

Duerden, J. E., and Ayres, S. A.

:05. The Nerve-layer in the Coral Coenopsammia. Seventh Report Mich. Acad. Sci., pp. 75-77. Jordan, H.

:07. Die Verdauung bei den Aktinien. Arch. f. ges. Physiol., Bd. 116, pp. 617-624.

Kassianow, N.

 Untersuchungen über das Nervensystem der Alcyonaria. Zeit. f. wiss. Zool., Bd. 90, pp. 478-535.

Parker, G. H.

:05a. The Reversal of Ciliary Movement in Metazoans. Amer. Jour. Physiol., vol. 13, no. 1, pp. 1-16.

Parker, G. H.

:05^b. The Reversal of the Effective Stroke of the Labial Cilia of Sea-Anemones by Organic Substances. Amer. Jour. Physiol., vol. 14, no. 1, pp. 1–6.

Parker, G. H.

 The Phylogenetic Origin of the Nervous System. Anat. Record, vol. 4, no. 2, pp. 51-58.

Pratt, Edith M.

:05. The Digestive Organs of the Aleyonaria and their Relation to the Mesogloeal Cell Plexus. Quart. Jour. Micr. Sci., vol. 49, n. s., no. 194, pp. 327-362.

Street, J. P.

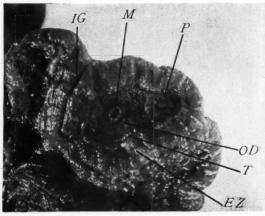
:08. Report of the Connecticut Agricultural Experiment Station. Food Products, 1908. Part of the Biennial Report of 1907–1908, pp. 573–762.

Verrill, A. E.

:02. Comparisons of the Bermudian, West Indian, and Brazilian Coral Faunae. Trans. Conn. Acad. Arts and Sci., vol. 11, pt. 1, pp. 169-206.







Small portion of a colony of Isophyllia showing oral surface of a partially

expanded polyp. \times 13. EZ, edge zone; IG, interpolypal groove; M, mouth; OD, oral disk; P, small polyp which has arisen by fission from the larger polyp on the left; T, tentacles.



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